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CTENOTUS KURNBUDJ AND CTENOTUS GAGUDJU, TWO NEW LIZARDS (SCINCIDAE) FROM THE ALLIGATOR RIVERS REGION OF THE NORTHERN TERRITORY

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ABSTRACT

Two new scincid lizards, *Ctenotus kurnbudj* sp. nov. and *Ctenotus gagudju*, sp. nov., are described and the distribution of both species in the Northern Territory is given. Distribution by habitat preference is discussed for eight species of *Ctenotus* Storr (*C. arnhemensis* Storr, *C. coggeri* Sadlier, *C. essingtonii* (Gray), *C. gagudju*, *C. inornatus* (Gray) *C. robustus* Storr, *C. storri* Rankin, *C. vertebralis* Rankin and Gillam) in the eastern Alligator Rivers region.

KEYWORDS: Scincidae, Australia, *Ctenotus*, taxonomy, new species, distribution, habitats.

INTRODUCTION

The reptile fauna of the Alligator Rivers region of the Northern Territory are now relatively well known (see Cogger 1974; Christian and Aldrick 1977). From later survey work a number of species endemic to the rocky escarpment habitat of Arnhem Land have been described (Cogger 1975; Gow 1977; King 1982; King and Gow 1983; Sadlier 1985). However, only in more recent years have lowland habitats of the Alligator and Wildman Rivers to the west of the Arnhem Land escarpment been thoroughly collected to reveal a number of new taxa (Storr 1981; King *et al.* 1982; Sadlier 1984).

The genus *Ctenotus* Storr occurs throughout mainland Australia and southern New Guinea but is most diverse in the arid regions (see Cogger 1983). Species of this genus are usually associated with areas of high temperatures and little ground vegetation. Such conditions characterize the seasonally-arid north of Australia during the dry season. In the Kakadu Fauna Survey which ineluded the Wildman and Alligator Rivers systems, nine *Ctenotus* species have been recorded, a species density near as high as (Storr 1980a; Pianka 1969a) or greater than (Storr 1978; Storr 1980b) areas of comparable size in the western arid zone of Australia. Two of the *Ctenotus* species eollected by the authors from the Wildman and Alligator Rivers systems are new to science. These species are here described and their habitat specificity analysed.

Specimens were examined from the Australian Museum (AM), Australian National Wildlife Collection (ANWC), Museum of Victoria (MV), Queensland Museum (QM) and Northern Territory Museum (NTM).

Ctenotus kurnbudj sp. nov. (Fig. 1)

Type material. HOLOTYPE - Australian National Wildlife Collection (ANWC) R3461, an adult from 16 km west of Kapalga on Arnhem Hwy Northern Territory, 12°46'S 132°15'E, collected by J. Wombey, 25 October 1980, PARATYPES - NORTHERN TERRITORY: ANWC R3462, collected 25 October 1980, AM R106843, collected 26 October 1980, AM R106843, collected 5 March 1982, ANWC R3883, collected 18 September 1982, all from same locality as holotype; ANWC R3880, Kapalga, near airstrip, 12°34'S 132°14'E, collected J. Estbergs, 5 August 1982; ANWC R3882, Wildman River area, 12°40'S 131°59'E, collected J. Estbergs, 23 August 1982.

Diagnosis. C. kurnbudj is distinguished from all other members of the genus by possessing the following combination of

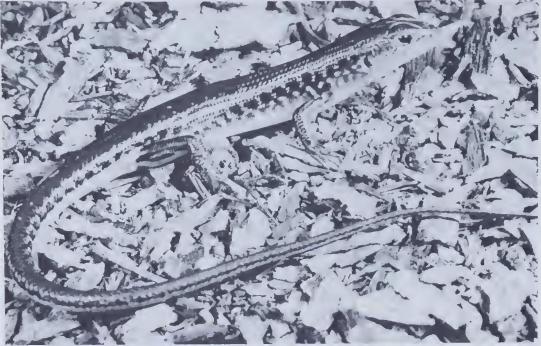


Fig. I. A live specimen of Ctenotus kurnbudj. Photo J. Wombey. scalation and colour characteristics: digits compressed with narrow, dark calli on the subdigital lamellae; frontal contacting first three of four supraoculars of which the second is widest; dark upper lateral zone enclosing several rows of fine spots; head and face reddish to light brown with scattered pale spots; no dark vertebral stripe; broad, dark laterodorsal stripe enclosing or alternating with a series of pale spots or blotches respectively, offset to a series of dark upper lateral blotches on tail (unique to C. kurnbudj).

The first four features in combination place C. kurnbudj in the C. leonhardii species group of Storr et. al (1981) while the last three features in combination will serve to distinguish C. kurnbudj from all members

of this species group. Description. This species is a medium sized Ctenotus attaining a maximum SVL of 54 mm.

Distance from axilla to groin 52-56.2% of SVL ($\overline{x} = 53.8, n = 6$); hindlimb length 52 -57.5% of SVL ($\bar{x} = 54.2, n = 7$); distance from forelimb to snout 38.8 - 44.4% of SVL $(\bar{x} = 42, n = 7)$; tail length 194.7 - 220.7% of SVL (n = 2).

Nasals narrowly separated or in point to narrow contact; prefrontals usually moderately separated (71%), otherwise

narrowly separated or in point contact; supraoculars four, first three contacting frontal; supraciliaries usually 8 (71.4%) or 7 (21.4%), rarely 9 (7.2%), first three largest and remainder, except for pentultimate (which is slightly larger), smaller and subequal; frontoparietals paired and distinct from interparietal; nuchals 3-6 either side $(\overline{x} = 4.6, sd = 1, n = 6)$; loreals two; upper and lower preoculars present, lower much the larger; anterior subocular single; upper labials 7 (57%) or 8 (43%) with fifth or sixth, respectively, subocular; postmental contacting first two lower labials on each side; ear opening large, vertically elliptic, usually with 5 (53.8%) or 4 (23%), rarely 3 or 6, broadly acute enlarged lobules anteriorly.

Midbody scale rows 26-30 ($\overline{x} = 28.7$, sd = 1.5, n = 6; paravertebral scales 54-67 ($\overline{x} =$ 62.5, sd = 4.1, n = 7), from first scale behind parietals to a point opposite the preanal scales; lamellae beneath fourth toe 23-28 ($\overline{x} = 26.4$, sd = 1.6, n = 7), moderately compressed and pale, each with a narrow dark callus.

Colour and pattern. Dorsal surface brown with moderately broad black laterodorsal stripes either enclosing a series of pale brown-white spots or broken into a series of alternate black and brown-white blotches.

Tail always with series of alternate light and dark laterodorsal blotches. A fine, pale dorsolateral stripe from above eye posteriorly to tail. Upper lateral zone black between ear and hindlimbs enclosing several series of longitudinally aligned white flecks, broken posterior to hindlimb into a series of black and brown blotches offset to those of laterodorsal stripe.

A fine, white midlateral stripe between fore and hindlimbs, broken over most of length. Lower lateral zone dark brown to black between limbs, light brown to grey with occassional white spotting anterior to forelimbs.

Hindlimbs brown with black longitudinally aligned stripes most often broken into elongate blotches. Venter pale. **Etymology.** 'Kurnbudj' is the name of the language group of the Aboriginal people who once occupied the area bordered by the upper reaches of the West Alligator River in the north, and lying between the South Alligator and middle reaches of the Wildman River in the south (Toohey 1981). The known distribution of *C. kurnbudj* occurs within this area.

Distribution. *C. kurnbudj* is recorded from four of the Kakadu Fauna Survey sites in the West Alligator - Wildman Rivers area (there were no other sites examined within the area defined by these four sites (Fig. 2).

Habitats. These four sites represent a range of woodland-open forest types which were intensively sampled on a total of six occasions during the three dry (August-

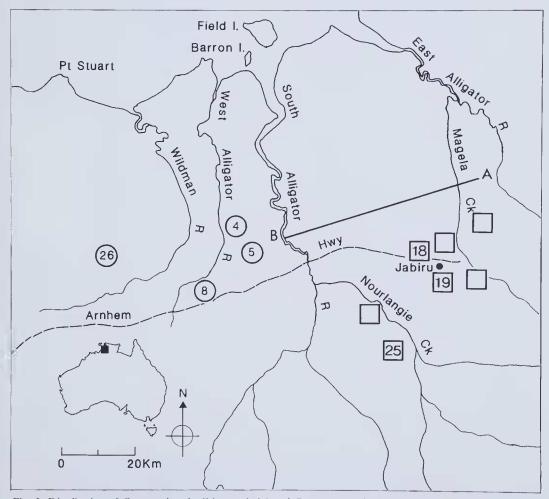


Fig. 2. Distribution of *Ctenotus kurnbudj* (open circle) and *Ctenotus gagudju* (open square) in the Alligator and Wildman Rivers regions. Note enclosed numbers are Kakadu Fauna Survey sites, and the line A-B represents the approximate line of the stylized transect of major habitats in Fig. 4.

November) and three wet (January-April) seasons of 1980-3. Details of the four localities follows:

Site 4: This site is a seasonally inundated riparian woodland with a total projective foliage cover (PFC, an index of foliage density) and PFC greater than three metres (an index of foliage density above 3 metres) of 71.7 and 17.4 (after Walker and Tunstall 1981) located in the Baker land system (Story *et al.* 1969) on brown massive earths. The main tree species were *Eucalyptus tectifica*, *E. clavigera*, *Planchonia careya* and *Erythrophleum chlorostachys*. The ground layer was dominated by a mixture of low sedges and grasses. The site was burned in three out of three years.

Sitc 5: This open forest has a total PFC and PFC greater than 3 m of 81.8 and 21.2. It is located in the Kay land system on yellow and red massive earths. The common tree species were *Eucalyptus tetrodonta*, *E. miniata* and *E. porrecta*. *Sorghum stipoideum* is dominant in the ground layer. The site was burned in two out of three years.

Site 8: The total PFC and PFC greater than 3 m of this open forest was 62.1 and 23. It is located in the Kay land system on brown massive earths. The common tree species were *E. miniata*, *E. tetrodonta* and *E. porrecta*. *S. stipoideum* was dominant in the ground layer. The site was burned in two out of three years.

Site 26: This site is a seasonally waterlogged woodland with total PFC and PFC greater than 3 m of 89.8 and 5.3. It is located in the Keefers Hut land system on brown massive earth and brown earthy sand. The main tree species were *E. tetrodonta*, *Erythrophleum chlorostachys*, *Pandanus spiralis* and *Petalostigma pubescens*. *S. stipoideum* was dominant in the ground layer. The site was burned in three out of three years.

Records of *C. kurnbudj* were acquired regularly on sites 5, 8 and 26 but the isolated records for site 4 suggest it may be sub-optimal habitat.

At all four sites *C. kurnbudj* was syntopic (occurring in the same habitat i.e. ecological sympatry) with *C. essingtoni* while at site 8 it also was syntopic with *C. robustus* and *C. arnhemensis* and at site 26 also with *C. robustus*.

Ctenotus gagudju sp. nov. (Fig. 3)

Type material. 11OLOTYPE - AM R97517 from Georgctown Billabong on the Magela Creek drainage system N.T., grid reference 5472-755975, 12°35'S 132°57'E, collected by R.A. Sadlier, March 1980. PARATYPES -NORTHERN TERRITORY: AM R88804-07, AM R88811-12, AM R88840-41, AM R88853-54, all from the Jabiluka project area, grid reference 5472-763080, 12°35'S 132°57'E; ANWC R3416, Jabiru area, site 19, 12°42'S 132°50'E; ANWC R2678, approximately 3 km south of Nourlangie Camp, 12°48'S 132°40'E.

All Australian Museum specimens collected on the Jabiru and Jabiluka uranium mining project areas, grid references refer to sheet No. 5472 (Edition 1) National Map Series, 'CAHILL'.

Additional material. NORTHERN TERRITORY: AM R88963-4 Jabiluka project area, grid reference 5472-763080, 12°35'S 132°57'E; ANWC R3417, 3421, 4327 Jabiru area, site 19, 12°42'S 132°50'E; ANWC R3380, 3889 Jabiru area, site 18, 12°39'S 132°48'E; ANWC R 2724, approximately 3 km south of Nourlangie Camp, 12°48'S 132°40'E; ANWC R2673, Oenpelli Road 3 km east of Nourlangie Camp turn off, 12°53'S 132°40'E; ANWC R3322, south of Mt Cahill, site 25, 12°54'S 132°42'E.

Diagnosis. C. gagudju is distinguished from all other members of the genus by the following combination of scalation and colour characteristics: frontoparietals fused to form single scale (unique in *Ctenotus*); digits compressed with a brown, obtuse to narrow keel on the subdigital lamellae: frontal contacting first three of four supraoculars of which the second supraocular is widest; dark laterodorsal stripc present, moderately narrow; pale midlateral stripe prominent and broken anteriorly; anterior part of body with predominance of reddish pigmentation on facial and anterior lateral surfaces and brown on dorsal surface.

The above features of scalation (except the first) align *C. gagudju* with the *C. leonhardii* species group. Within this group, *C. gagudju* is most similar to *C. hilli* (of which we have only seen preserved material and a colour transparency).

C. gagudju and *C. hilli* differ from all but three other members of the *C. leonhardii* species group in having the black vertebral stripe, if present narrow and without pale cdging, the dark laterodorsal stripe un-

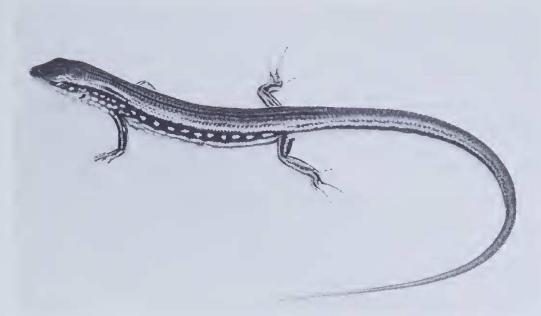


Fig. 3. A live specimen of *Ctenotus gagudju* (holotype) from Georgetown Billabong on Magela Creek. Photo R. Sadlier.

marked and present as a moderately narrow edging to paler dorsolateral stripe, and the dark upper lateral zone with single row of distinct white blotches. In the C. leonhardii species group, this combination of characters is shared only with C. alleni, some C. mimetes and C. regius. C. hilli and C. gagudju differ from these three species in having the prefrontals moderately to widely separated instead of contacting. C. gagudju differs from C. hilli in having the frontoparietals fused instead of divided. Otherwise measurements and meristies are similar for both species. The presence or absence of a dark vertebral stripe is variable in both species. However, the pale midlateral stripe is nearly always continuous in C. hilli but variably broken for the entire length or only anteriorly into a series of dashes in C. gagudju.

Description. This species is a medium sized *Ctenotus* attaining a maximum SVL of 54 mm.

Distance from axilla to groin 51.6-61.1% of SVL ($\bar{x} = 57.1$, n = 13); hindlimb length 45.3-56.6% of SVL ($\bar{x} = 51$, n = 13); distance from forelimb to snout 33.3-42. 4% of SVL ($\bar{x} = 38$, n = 13); tail length 206.1-238.8% of SVL ($\bar{x} = 223.1$, n = 6).

Nasals usually in moderate to broad contact (92.3%), rarely in point contact (7.7%); prefrontals moderately to widely

separated; supraoeulars four, first three eontacting frontal; frontoparietals fused to form a single scale distinct from interparietal (except ANWC 3380 where interparietal is fused to frontoparietal); supracilliaries usually 7 (84.6%) rarely 8 (15.4%), first three largest and remainder, except for pentultimate, smaller and more or less equal in size; nuchals 2-5 either side $(\bar{x} = 3.6, sd = 0.9, n = 13)$; loreals two; upper and lower preceulars present, lower larger; anterior subocular single; upper labials 7, fifth subocular; lower labials 6, postmental contacting first two on each side; ear opening moderately large with 4 (61.5%) to 5 (38.5%) pale, acute lobules anteriorly, the middle most of which is largest.

Midbody seale rows 28-32 ($\overline{x} = 30.5$, sd = 1.2, N = 13); paravertebral scales 55- 68 ($\overline{x} = 59.2$, sd = 3.6, n = 12); lamellae beneath fourth toe 21 - 28 ($\overline{x} = 23.6$, sd = 1.6, n = 13), moderately compressed with obtuse to narrow darker calli.

Colour and pattern, Dorsal surface brown, with (holotype) or without (paratypes) narrow black vertebral stripe from nape to just past level of hindlimbs. A fine, pale, dorsolateral stripe full length of body and original tail, in life with yellow flush over most its length, bordered above by a moderately narrow black laterodorsal stripe. Upper lateral zone dark brown anteriorly, becoming black posterior to ear opening and extending along tail, enclosing a single row of distinct white blotches from rear of cye to level of hindlimbs. Pale midlateral stripe broken anteriorly, continuous from mid-dorsum to groin, in life with yellow flush posteriorly. Lower lateral zone russet with irregularly scattered pale blotches. Fore and hindlimbs with alternate dark and pale longitudinal striping, soles of feet pale. Venter cream.

Etymology. 'Gagudju' is the name of the language group of the Aboriginal people who traditionally inhabited the northern half of the area between the South Alligator and East Alligator Rivers (Toohey 1981). The known distribution of *C. gagudju* occurs within this area, most of which is now included in the recently dcclared Kakadu National Park. 'Kadkadu', a corruption of 'gagudju', is the name recorded by Specer (1914) for those Aboriginals, whose descendants still live in the area.

Distribution. *C. gagudju* is known from lowland woodland associated with the upper reaches of Magela Creek (tributary of East Alligator River) and the mid to upper reaches of Nourlangie Creek (tributary of South Alligator River), both of which run from the western edge of the Arnhem Land escarpment

Habitats. Specimens from the Jabiluka and Jabiru uranium mining project areas were collected in mixed cucalypt woodland on a hard lateritic substrate. The Jabiluka site is gently undulating lowland crisscrossed with low drainage channels leading to tributaries of Magela Creek. Here, domintree species are E, miniata, E. ant tetrodonta, E. bleeseri and E. porrecta to 14 metres height, evenly distributed with a gap size of 7 metres and a canopy cover of 25%. The shrub layer is relatively dense with the species (Planchonia careya, Petalostigma pubescens) evenly distributed, intervening ground cover is dominated by Sorghum sp. which occurs as unburnt patches during the dry season.

Sites on or near the Jabiru project area (in the vicinity of Georgetown Billabong, 009 gauge station on Magela Creck, and sites 18 and 19 of the CSIRO Kadadu Survey) and further to the south and west on Nourlangie Creek, are on undulating lowland dissected by seasonally dry drainage channels. Here the dominant tree species, *E. bleeseri* to 16 metres height (with saplings 6-8 metres) and *Xanthostemon paradoxum* to 6-12 metres height, are widely spaced. The shrub layer (*P. pubescens, Acacia* sp.) is sparse and the intervening ground cover dominated by expanses of *Sorghum* sp. and low sparse grasses.

C. gagudju is the only *Ctenotus* species recorded in type 1 mixed eucalypt woodland as described by Burgman and Thompson (1982), which features a hard, reddish lateritic substrate. Where this habitat approaches the riparian fringes bordering tributaries of Magela Creek *C. gagudju* is paratopic (i.e. occurring in adjacent habitats without overlap) with *C. essingtonii* and *C. robustus* which occur in dryland associated riparian communities on sand and silt substrate.

Reproduction. Adult females collected during the dry season of 1978 (August to September) showed no sign of reproductive activity while a single female collected during the wet season (March 1981) had three moderately enlarged yolked ovarian follicles (1 in left oviduct, 2 in right).

Ctenotus hilli Storr

Type material. PARATYPES - NORTHERN TERRITORY: QM J2615, 2617, Darwin, 12°27'S 130°50'E; MV D1652, Bathurst Island; MV D5146, upper Roper River; MV D12371-72, Darwin.

Additional material. NORTHERN TERRITORY: AM R75235, upper reaches of McKinlay River 13°17'S 131°43'E; NTM R8115-17, 17 mile Darwin, 12°32'S 131°0 3'E.

Distribution. C. hilli occurs in the far northwestern sector of the Northern Territory (including Bathurst Island) except for a record from the 'upper Roper River' presumably on the southwestern edge of Arnhem Land (NMV D 5146). The specimen of C. hilli geographically closest to C. gagudju is from near Mt. Douglas (13°15'S 131°44'E) on the southern end of the Mount Bundy Ranges N.T., (some 150 km west of the distribution of C. gagudju), this specimen was collected at the very foot of a rocky hill with sparse covering of vegetation.

HABITAT PREFERENCES OF CTENOTUS SPECIES IN ALLIGATOR RIVERS REGION.

Ctenotus is the largest Australian seincid genus with 68 speeies recorded by Cogger (1983). The genus is well documented on a regional basis in Western Australia (see bibliography of Storr *et al.* 1981) where it is most diverse, being represented in certain regions by a number of species some of which may occur in ecological sympatry (syntopy).

Pianka (1969b) published on the ecology of *Ctenotus* in the southwest arid regions of Australia and reported the occurrence of eleven species of desert- inhabiting *Ctenotus* in the one region of which seven sandplain dwelling species were syntopic. Brief notes on distribution have appeared in taxonomic studies of *Ctenotus* from the 'Top End' (Storr 1970; Rankin 1978; Rankin and topie (1. C. coggeri and C. inornatus, 2. C. essingtonii and C. vertebralis, 3. C. essingtonii and C. robustus) and one example of three species syntopic (C. essingtonii, C. arnhemensis and C. storri).

Here we examine the habitat preferences of the eight species in the East and South Alligator Rivers region by elaborating on the data figured by Cogger (1982: 154, fig. 2) and here modified in Fig. 4 as a stylized transect from an escarpment outlier west across the Magela Creek and surrounding floodplain and lowlands to the South Alligator River.

Habitat includes topographic features and vegetative structure and floristics as defined by Burgman and Thompson (1982), as these features combine to influence the distribu-

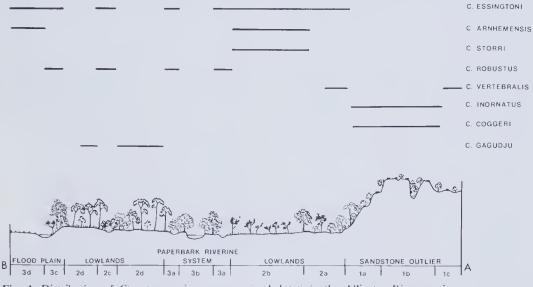


Fig. 4. Distribution of Ctenotus species across major habitats in the Alligator Rivers region

Gillam 1979) but nothing of habitat preference has been documented for the genus in a regional context.

The eight species of *Ctenotus* known from our studies in the East and South Alligator Rivers region represent one modcrately small species (*C. storri* maximum SVL 40.5 mm), four medium sized species (*C. arnhemensis* maximum SVL 56 mm, *C. essingtonii* maximum SVL 61 mm, *C. vertebralis* maximum SVL 55mm, *C. gagudju* maximum SVL 54 mm) and three large species (*C. coggeri* maximum SVL 80 mm, *C. inornatus* maximum SVL 75 mm, *C. robustus* maximum SVL 110 mm). We recorded three examples where two species are syntion of the reptile fauna in the area. Major habitats surveyed in the Alligator Rivers region follow:

(1). Sandstone outcroppings or outlicrs of the Arnhem Land escarpment (i.e. Cannon Hill, Djawamba massif, Mt Brockman and Nourlangie Rock) have sandstone type vegetation communities. The escarpment area of the sandstone outlier is comprised mainly of jumbled outcroppings with little exposed soil (Fig. 4, la), and the plateau comprises large boulders and bluffs (Fig. 4, lb,) but occasionally with open woodland areas free of boulders (Fig. 4, le),

(2). There are four main dryland habitats of the lowlands. 2a): Type 3 mixed eucalypt

woodland community borders the sandstone escarpment (Fig. 4, 2a) and extends onto the outwash areas, here the substrate is sandy. 2b): Fabaceous- myrtaceous open woodland is located along slowly flowing seasonal creeks and rivers (Fig. 4, 2b) the substrate is sand-silt. 2c): Dryland associated riparian woodland (Fig. 4, 2c) is associated with seasonal watercourses and has a substrate of sand-silt. 2d): Type 1 mixed eucalypt woodland is the most widespread community on undulating lowland away from the sandstone outlier and riverine floodplain (Fig. 4, 2d), here the substrate is a hard laterite.

(3). Wetland habitat includes riparian woodland (Fig. 4, 3a) and paperbark woodland (Fig. 4, 3b) associated with the paperbark riverine system, and riparian woodland (Fig. 4, 3c) and open grassland (Fig. 4, 3d) communities associated with the floodplain.

On the sandstone outlier *C. inornatus* and *C. coggeri*, are syntopic and restricted to boulder slopes of the escarpment, and in rocky areas of sandstone plateaux. In wooded areas of the sandstone plateaux away from rock outcroppings *C. vertebralis* occurs, here it is paratopic with *C. inornatus* and *C. coggeri*.

The most widespread species in lowland habitats is *C. essingtonii*, occurring in habitats bordering the escarpment, dryland associated riparian woodland, fabaceousmyrtaceous open woodland, and floodplain associated riparian woodland and grassland communities,

In type 3 mixed eucalypt woodland communities on sandy substrate bordering the base of the outliers and on outwash areas of the outliers, *C. vertebralis* and *C. essingtonii* are syntopic. In fabaceous-myrtaceous woodland *C. essingtonii* is syntopic with *C. arnhemensis* and *C. storri*, two recently described species (Storr 1981 and Rankin 1979 respectively).

In type 1 mixed eucalypt woodland C. gagudju is the only Ctenotus species.

Seasonally dry creek channels pass through type 1 mixed eucalypt woodland communities. In dryland riparian communities bordering these creek channels, C.*essingtonii* and *C. robustus* are syntopic and both are paratopic with *C. gagudju* which occurs in the immediately adjacent type 1 mixed eucalypt woodland.

In riparian woodland communities associated with paperbark riverine systems C. essingtonii and C. robustus are syntopic. In open grassland associated with the upper floodplain fringe and bordering billabongs of the mid reaches of Magela crcek, C. essingtonii and C. arnhemensis are syntopic. No Ctenotus species occur in paperbark woodland associated with the paperbark riverine system.

From the type description by Rankin and Gillam (1979) C. vertebralis is known from three localities along the western and southern borders of Arnhem Land. All localities are open woodland in close association with rock outcropping on lateritic to sandy soils. Notes by Gillam (cited by Rankin and Gillam 1979) indicate C. vertebralis may be replaced by Ctenotus spaldingi in rocky areas on the Cox River Station while notes by Cogger and Wombey (cited by Rankin and Gillam 1979) indicate C. vertebralis was not collected in rocky areas at Mr Brockman.

Our observations confirm the absence of *C. vertebralis* from rocky habitat.

Much of the diversity of Ctenotus species in the Alligator Rivers region is explained by the diversity of habitats in the region and within habitats by the size difference between species. However several similarly sized species occur syntopically (l. C. coggeri and C. inornatus, 2. C. essingtonii and C. vertebralis, 3. C. essingtonii and C. arnhemensis and their syntopy obviously cannot be explained by habitat or size differences. Pianka (1969b) has shown that similarly sized desert dwelling Ctenotus species partition resources in other ways: microhabitat, food, activity period and these may operate to explain the coexistence of similar sized, syntopic Ctenotus species in the Alligator Rivers region.

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Mrs Tina Goh typed the various drafts of the manuscript. Ms D. Kent prepared Fig. 4; and jointly with F. Knight Fig. 2.

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